DISJUNCTIONS IN BRYOPHYTES

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ABSTRACT

In spite of the more general distribution of many bryophytes, dramatic disjunctions exist, many of them similar to those shown by vascular plants. Various explanations have been offered to explain these disjunctions including continental drift, long-distance dispersal, and the fragmentation of a once more continuous distribution. No single hypothesis is sufficient to accommodate all species within any disjunctive pattern. The most serious difficulty is the inadequacy of exploration of considerable areas of the globe.

Various bryophyte disjunctions are mapped in 51 distribution maps, and details of sexual

patterns and dispersal mechanisms are assessed.

Most bryophytes are widely distributed. In the Northern Hemisphere more than 60% of the flora of arctic and boreal regions is made up of the same species. Within this wide range, however, each species has highly specific requirements and some are exceedingly local.

Because bryophytes have air-borne diaspores their means of dissemination would appear to guarantee a wide distribution of all species. That disjunctions exist at all would seem somewhat anomalous, yet such disjunctions do exist, some of them very dramatic. The explanation of these disjunctions has led to numerous intriguing hypotheses, many of which have been derived from similar studies of flowering plant disjunctions.

In North America the disjunctions that have received the greatest attention are eastern American-East Asian disjuncts (Iwatsuki, 1958a, 1958b, 1958c; Iwatsuki & Sharp, 1967, 1968; Sharp & Iwatsuki, 1965. See Maps 1-7); tropical and subtropical taxa in the Southern Appalachians (Anderson, 1951; Andrews, 1920; Billings & Anderson, 1966; Crum, 1966; Sharp, 1936, 1938, 1939, 1941. See Maps 8-9); amphi-Pacific taxa (Ando, 1966; Ando, Persson & Sherrard, 1957; Crum, 1965; Hattori, 1952, 1963, 1966b; Hattori & Sharp, 1968; Hattori et al., 1968; Horikawa & Ando, 1957; Lazarenko, 1957; Noguchi & Saito, 1970; Persson, 1946a, 1946b, 1947, 1949, 1952, 1958, 1962, 1968; Persson & Gjaervoll, 1957; Schofield, 1962, 1965, 1966a, 1966b, 1966c, 1968a, 1968b, 1969; Sharp & Hattori, 1967; Steere, 1969; Steere & Schofield, 1956; Steere & Schuster, 1960. See Maps 10-20); bipolar disjuncts (Martin, 1946, 1949, 1952a, 1952b; Du Rietz, 1940; Sainsbury, 1942; Schuster, 1969. See Maps 21-22); taxa disjunctive between Europe and western North America (Abramova & Dildarin, 1969; Evans, 1914; Harvill, 1950; Haynes, 1915; Koch, 1956; Paton, 1966; Schofield, 1968a, 1968b, 1969; Whitehouse, 1961, 1963. See Maps 23-33); amphi-Atlantic taxa (Andrews, 1938, 1961; Maass, 1965, 1966a, 1966b; Schuster, 1962; Sharp, 1941. See Maps 34-37); and arctic-alpine taxa, that have received surprisingly little attention (Gams, 1955; Schuster, 1958a, 1958b; Steere, 1937, 1938, 1953, 1965. See Maps 38-40).

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Irmscher (1929) studied moss disjunctions particularly in their contribution to an insight reflecting plant distributions as influenced by continental drift. Herzog (1926) in his monumental *Geographie der Moose* treats bryophyte disjunctions briefly. Details from other areas are treated by Abramova & Abramov (1969), Bowers (1970), Croizat (1962, 1966), Crum (1966), Crum & Anderson (1964), Fulford (1951), Greig-Smith (1950), Horikawa (1955), Koch (1954), Lazarenko (1957), Müller (1916, 1954), Schelpe (1969), Schofield (1969), and Schuster (1967, 1968, 1969).

Hypotheses explaining these disjunctions have been based mainly on historical factors. In most cases the opinion is that these various disjunct populations represent remnants of a more continuous distribution of the past, always placed preceding the Pleistocene glaciations and usually suggested to be as early as the Tertiary. Information from fossil bryophyte material is generally sparse; thus the assumption is made that bryophytes were associated with a vascular vegetation which exhibited a more continuous distribution during the Tertiary.

One bryophyte showing disjunctive European–western North American distribution is Claopodium whippleanum (Noguchi, 1952. See Map 33). The species is also present in the Hawaiian Islands. Abramova and Abramov (1969) indicate that they discovered it as fossil material from Middle Pliocene deposits in the Caucasus region. In Europe the species is presently restricted to a number of localities in Portugal and Spain. Another species of similar distribution, but with the Caucasus showing the only extant European population, is Crumia latifolia (see Map 26). This is discussed by Abramova and Dildarin (1969). These distributions strongly suggest a more continuous distribution of the past.

Remarkable features of a high proportion of disjunctive species is that they are dioicous and in many cases produce no specialized propagula that would make them readily disseminated. This complete reliance on asexual reproduction by simple fragmentation leads to a paucity of biotypes. These combined features mean that the disjuncts tend to be, within their disjunctive areas, highly localized as relatively small populations with very specific environmental requirements. In most cases they are very poor competitors with the more generally distributed flora and are often confined to sites that are continually undergoing ecesis (Lye, 1967).

Areas particularly rich in disjunctive taxa often have hyperoceanic climates. This subject has been treated thoroughly by Ratcliffe (1968) and Størmer (1969) in particular, but also discussed by Amann (1929), Billings and Anderson (1966), Courtejaire (1962), Gaume (1952–1954), Iwatsuki (1958a), Lye (1967), Nicholson (1930), Persson (1949), Schuster (1962), and Touffet (1964).

The areas richest in disjunctive species confined largely to hyperoceanic climates are: Britain and Norway, the Faeroes, the Alps, the Himalayas, high mountains of Japan and Taiwan, North Pacific North America, and to a certain degree, high mountain slopes in the Hawaiian Islands. In some cases identical disjunctive species are found in many of these widely separated areas, for example: Geheebia gigantea (Map 41), Mastigophora woodsii (Map 42), Scapania ornithopodioides (Map 43), Anastrepta orcadensis (Map 44), Anastrophyllum donianum (Map 45), Pleurozia purpurea (Map 46), Bazzania pearsonii, Cephaloziella pear-

sonii, Campylopus atrovirens, and others. Species of the East Asian-eastern American disjunction, the European-western American disjunction and amphi-Pacific disjunction are also largely of oceanic climates.

In the Southern Hemisphere disjunctions are also richly represented in hyperoceanic climates: the southern Australasian–southern South American disjunction is the most pertinent example, shown in Maps 47–48 (see especially Schuster, 1969).

Disjuncts of more arid climates are equally dramatic: thus the isolation in Australasia and South Africa represented by *Carrpos sphaerocarpos* (Map 49) of arid salt pans and *Pottia maritima* (Map 50) of sandy sites. These species, however, are either very rare or are overlooked because of their inconspicuousness. As Schelpe (1969) has shown, the number of bryophytes of this disjunctive pattern may increase as both areas become better collected.

Species of mediterranean climates exemplify yet another type of disjunction. Neckera menziesii, Antitrichia californica (Map 32), Funaria muehlenbergii, and Bartramia stricta are particularly good examples. The Neckera is largely mediterranean in Eurasia and North Africa but in western North America is both in mediterranean and more humid climates, but in the more humid climates is confined largely to edaphically dry calcareous rock; it is rare in Japan. Antitrichia shows a similar pattern but is absent from Japan.

As has been noted (Sharp, 1938; Schornherst, 1943), many bryophytes of tropical affinity disjunctive in more northern areas tend to be calcicoles. Considering the Florida moss flora, Schornherst (1943) suggests that this may be the result of the frequency of this habitat in the tropics, thus the selection favoring bryophytes of this specificity.

In spore-producing plants there is an obvious temptation to state that long-distance dispersal is especially important. Spore size enhances wind-dispersal and air transport of spores is necessary even in short-distance dissemination of most spore-bearing plants.

In bryophytes it is apparent that long-distance dispersal is not only possible, but in some cases probable. Certainly the taxa of volcanic oceanic islands reached their present sites via long-distance dispersal. Although published analyses of the Hawaiian bryoflora are lacking, this archipelago could serve as a particularly important source of information concerning long-distance dispersal in bryophytes. The archipelago is relatively youthful, emerging no earlier than the Late Tertiary, thus has been available for colonization for approximately ten million years. A number of disjunctive bryophytes are of particular interest: Cyrtopus setosus (Map 48) is otherwise a species of the Southern Hemisphere. Dixon (1922) has established the authenticity of the Hawaiian collection of the species, but it has not been recollected recently. The hyperoceanic taxa Scapania ornithopodioides (Map 43) and Anastrepta orcadensis (Map 44), in particular, are of considerable significance. These are both dioicous and sporophytes are rare or unknown. Gemmae are present in only the Anastrepta, and the Scapania has no specialized vegetative disseminules. It must be assumed that the species did produce sporophytes in the past, and it would be reasonable to assume that the species were then more widespread. If rare, even in the past, their chances of establishing their many widely disjunct populations would be so greatly reduced as to be unreasonable. The added problems of disseminules taken from the parental population of a humid environment, drawn into updraughts of air and then carried to a favourable site (which for these species is highly specialized) make the chances of long-distance dispersal even more unlikely. Yet the species are present in areas that they could not have reached except by wind-dispersal from sources a considerable distance away.

Størmer (1969) has outlined a clear instance of long-distance dispersal in the moss *Orthodontium lineare*. Although not so spectacular as the Hawaiian disjunction, this case is well documented. *Orthodontium lineare* was inadvertently introduced to the Liverpool district of Great Britain around 1911. The species has spread rapidly through Britain, by 1963 being present in most vice counties in England and reported also in Scotland and Ireland. In 1952 the species was reported from Holland, where "the spores must have been carried 300 km or more before they found suitable habitation" (Størmer, 1969). In 1939 the species was discovered in Germany, presumably derived from the British populations. In many cases, at least, the expansion of the range of this species must be ascribed to wind dispersal of the spores.

Considerable discussion was elicited by the paper of Petterson (1940) concerning the long-distance dispersal of the mosses Aloina brevirostris and A. rigida from Siberia to southwestern Finland, where he had recovered numerous spores of the species in rainwater. Persson (1944) and Bergeron (1944) have demonstrated the greater likelihood that the spores originated from nearby Scandinavian populations. The fact that moss spores serve as nuclei for rain drops is of particular importance, however, and should not be overlooked. The discussions of both Bergeron (1944) and Gregory (1945) are especially rich in information concerning dispersion of air borne spores.

In a few cases bryophytes are disjunctive because they have been introduced to their widely separated localities through man's activities. The hepatics Lunularia cruciata and Marchantia polymorpha are common greenhouse weeds and are widely dispersed throughout the world because of this. More precisely documented cases are those for Tortula stanfordensis (Map 31) and Pseudoscleropodium purum (Map 51). The Tortula was described by Steere (1951) from the San Francisco Bay Region of California where it is widely distributed on hard clayey soil both near habitations and in the native vegetation. Paton (1966) reported this species from southern Britain. More recently further details have appeared concerning its British distribution (Whitehouse, 1961; Whitehouse & Paton, 1963). In the latter publication the authors state "since both Mousehole and Gulval are centres for the horticultural and market gardening industries, it seems possible that Tortula stanfordensis may have been accidentally introduced to one or both of these areas from California." It is suggested that it might have been introduced in soil of planted trees originating from a Californian nursery.

For *Pseudoscleropodium* the disjunctions are equally interesting and are discussed by Dickson (1967); details for the western American localities are given by Lawton (1960) and Schofield (1965), while the New Zealand populations are discussed by Sainsbury (1935, 1955). Dickson states that the species was probably

Table 1. Sexuality of disjunct bryophyte taxa. A plus sign (+) indicates that most disjunctive species are sterile. An asterisk (*) indicates that the species is consistently or usually sterile.

Monoicous	Dioicous
Desmatodon randii	Pterogonium gracile
Pottia maritima	Echinodium (the genus)
Sphagnum junghuhnianum	+ Myurium (the genus)
(also dioicous)	Phyllogonium (the genus)
Grimmia olympica	Drepanocladus uncinatus
Aulacomnium heterostichum	Hylocomium splendens
Buxbaumia minakatae	Cyrtopus setosus
Hookeria lucens	* Tortula caroliniana
Cephaloziella turneri	* Leptodontium orcuttii
(also dioicous)	* Gollania turgens
Pleurozia purpurea	
Tieurosia purparea	Sphagnum junghuhnianum
	(also monoicous)
	+ Acanthocladium (sect. Tanythrix)
	Oligotrichum hercynicum
	* Geheebia gigantea
	Drummondia prorepens
	* Homaliadelphus sharpii
	* Schwetschkeopsis fabronia
	Atrichum crispum
	Sphagnum angermanicum
	* S. pylaesii
	* Ditrichum zonatum
	Plagiothecium undulatum
	* Crumia latifolia
	* Leptodontium recurvifolium
	Antitrichia californica
	Polytrichum sphaerothecium
	* Acrobolbus ciliatus
	* Mastigophora woodsii
	* Anastrepta orcadensis
	* Scapania ornithopodioides
	Bucegia romanica
	Porella cordaeana
	* Cephaloziella turneri (also monoicous)
	* Plagiochila japonica * Badula auriculata
	randa and canal
	Carrpos sphaerocarpos
	* Ascidota blepharophylla
	* Anastrophyllum donianum
	Haplomitrium hookeri
	* Takakia ceratophylla
	* Macrodiplophyllum plicatum
	* Plagiochila carringtonii

introduced to the south Atlantic islands of St. Helena and Tristan da Cunha as packing material of young trees. In western North America the species is a lawn weed and is always associated with human habitation, thus a probable introduction with nursery stock from Europe. The case for New Zealand is less clear, most populations being confined to areas near human habitation, but "the Tasman finding was in *Leptospermum* scrub and would be more likely to indicate an indigenous moss" (Sainsbury, 1955).

As mentioned earlier, a high proportion of disjunct bryophytes are dioicous. In some cases, the male plant is in one of the areas of disjunction and the female plant in another: *Acrobolbus ciliatus* (Map 7) is male in Japan, female in the Southern Appalachians. In such cases the only reasonable explanation for the disjunction is to assume that both arose from an originally continuous population. Why one sex should survive in one region and the other in the second is not readily explained. *Homaliadelphus sharpii* (Map 2) would appear to be sterile in North America but fertile in eastern Asia. However, dwarf male plants have been found in two North American populations, and therefore it is obvious that spores have been produced there, though indeed rarely.

In dioicous species of mosses specialized means of asexual production are no more frequent than in monoicous species whose ranges tend to be wider (Gemmell, 1952). The wider range of the monoicous species is presumably more a reflection of their spore dispersal than their greatly increased variability. As Gemmell (1950) has noted, it appears that many of the monoicous species are self-fertilized, greatly decreasing the possible variability that would be available through cross fertilization.

For species occupying open areas and in which either spores or gemmae are produced, the chances of wind dispersal are greatly improved, and in areas of relatively dry climates, the possibility of getting propagula air-borne is even greater. As Persson (1944) and Petterson (1940) have shown, such spores are air transported and can come to earth in rainfall some distance from their place of origin. The problem if their germination and survival in the place where they are deposited is much more uncertain. Since most bryophytes are ecologically restricted and conditions favoring germination and survival of propagula are highly critical, the chances that many air-transported propagula survive to establish a colony are very remote. The factors severely limiting the effectiveness of distance dispersal are discussed by Crum (1966, 1972).

A further complication is the fact that many disjunctive taxa are in hyperoceanic climates. This further decreases the opportunities for propagula to become air-borne in the rare cases when they are produced. Added to this is their restrictive ecology. Lye (1966) has emphasized that oceanic bryophytes are commonest "in localities where topography prevents both wind and sunshine from reaching high intensities."

It might be suggested that some bryophytes appear to be disjunctively distributed merely because collections have been inadequate in the intervening areas. Although this may prove to be true for a number of species now considered disjunctive, it is not likely to greatly decrease the number. In areas relatively thoroughly explored as for example, Europe, the disjunctive patterns have been maintained even after increased knowledge of the area. The absence of suitable habitats in the intervening areas also makes their possible presence in them very doubtful.

A knowledge of the details concerning continental drift is unlikely to be helpful in explaining most disjunctions in the Northern Hemisphere. In the Southern Hemisphere, however, Schuster (1969) suggests that the disjunctions are readily accommodated by the notion of a large Gondwanaland continent. It is also believed that many of the disjunctive taxa are extremely ancient, perhaps dating back to these earliest times. As frequently emphasized, bryophytes appear to be extremely conservative, controlled both by their inbreeding and by infrequency of sexual reproduction in many.

No single hypothesis can explain all disjunctions. Each hypothesis when ap-

plied to all disjuncts raises a number of serious questions.

First, assuming that long-distance dispersal is the answer:

1. Why has dispersal been so selective for taxa that now possess such inefficient means of dissemination and are presumably poor in biotypes?

2. Why should so many disjuncts be confined to oceanic environments?

3. Two areas possessing disjunctive species also have many species endemic to them that are widespread there, ecologically diverse and have ready means of airdissemination, yet in both cases these species have not reached the other disjunctive area. The problem is: why not?

Second, assuming that the disjunctive bryophytes represent remnants of an ancient flora that has persisted in or near the present location of the disjunctive population:

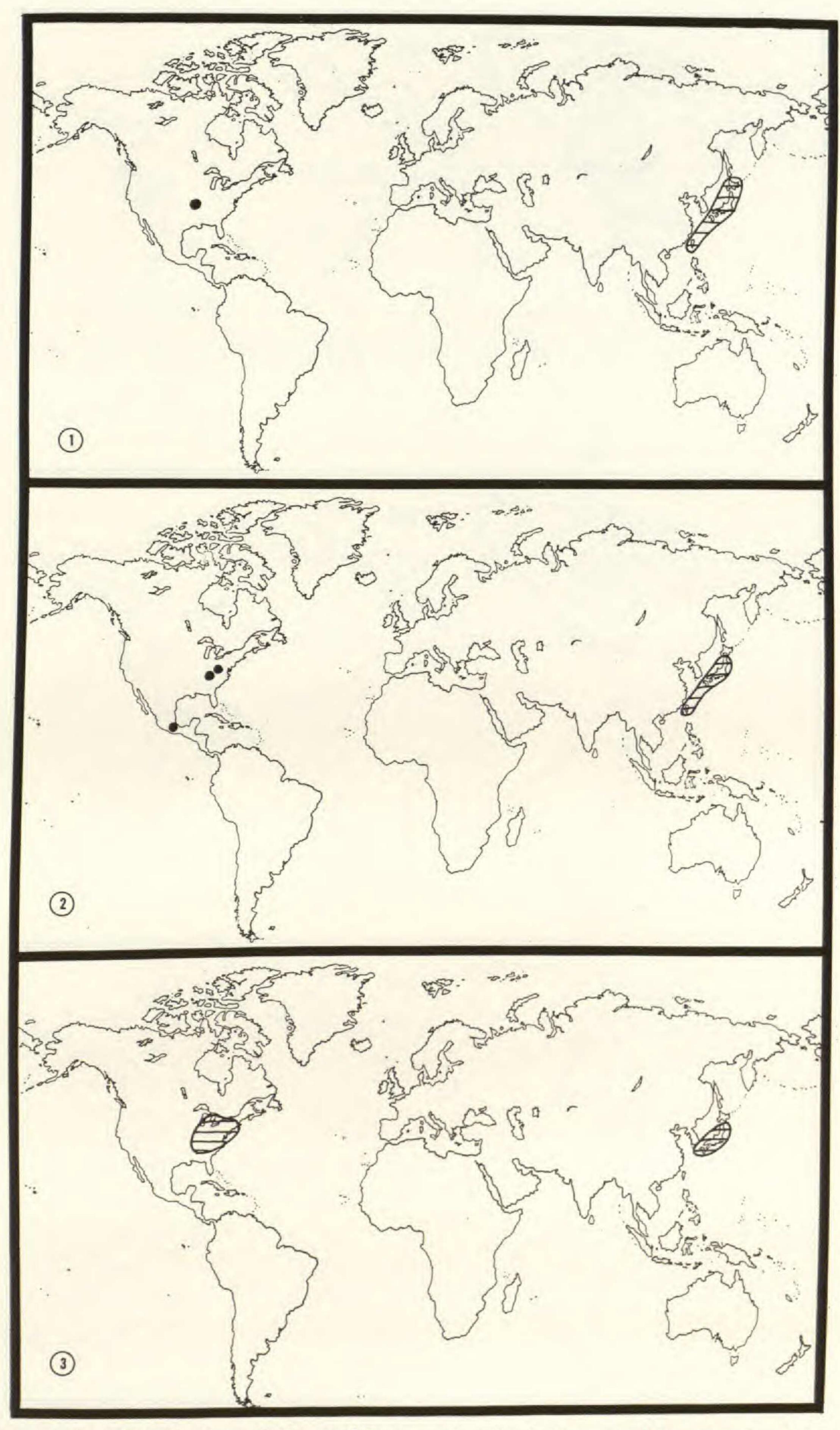
1. Why should some of the disjunctive species now exist in areas that have been available for only the time since the Pleistocene glaciations?

2. Since a number of disjuncts that presently lack any diaspores that are readily air-transported are now present on oceanic islands where they must have arrived by air, why could not other disjuncts have reached their sites in the same manner?

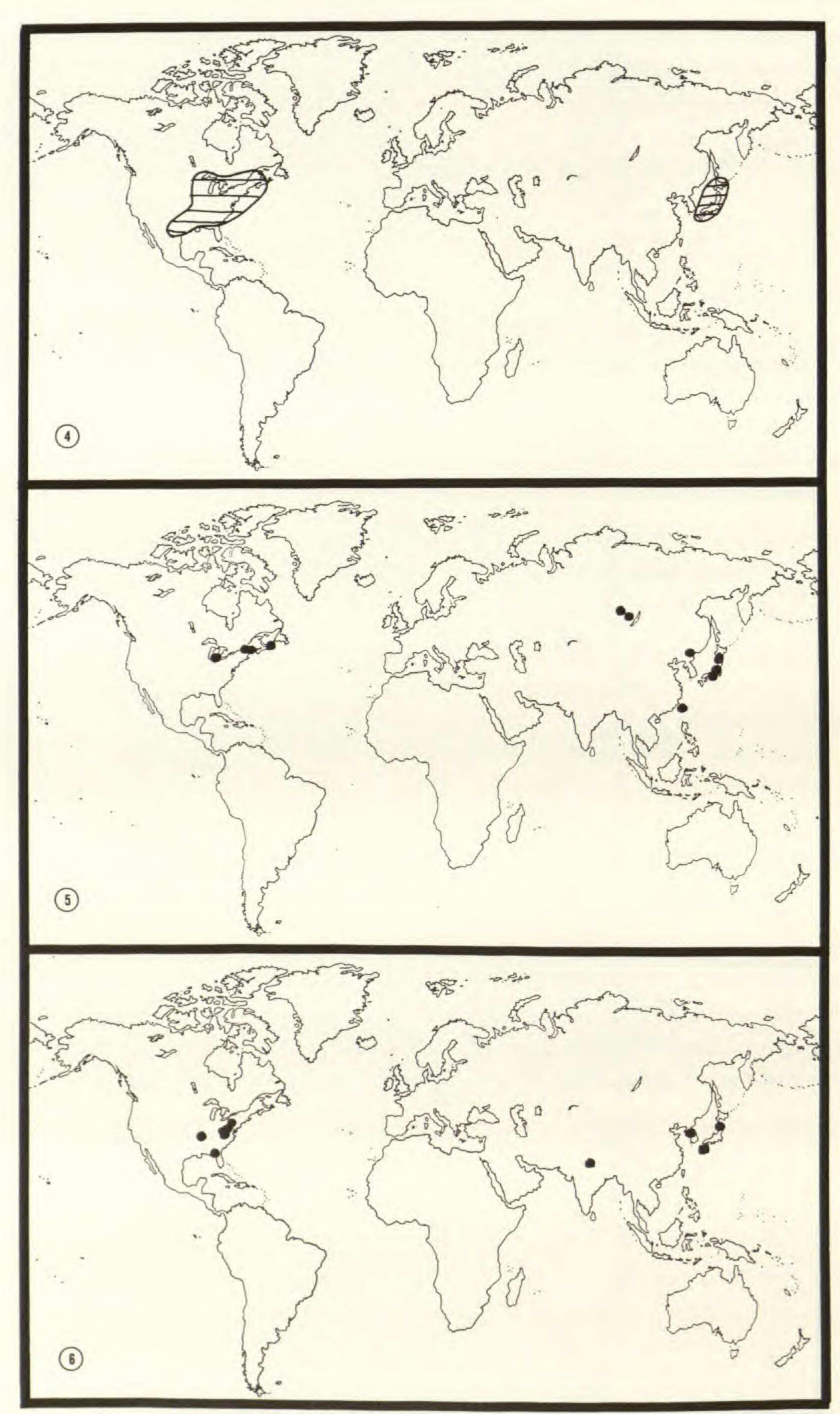
Third, assuming that continental drift has led to the establishment of the disjunctions:

Although this would be satisfactory for the amphi-Atlantic species, it creates further difficulties in attempting to explain the western North American—western European disjunction and the eastern North American—eastern Asian disjunction. It also poses serious problems in explaining the amphi-Pacific taxa, since preceding continental drift, these continental masses would have been even more distant.

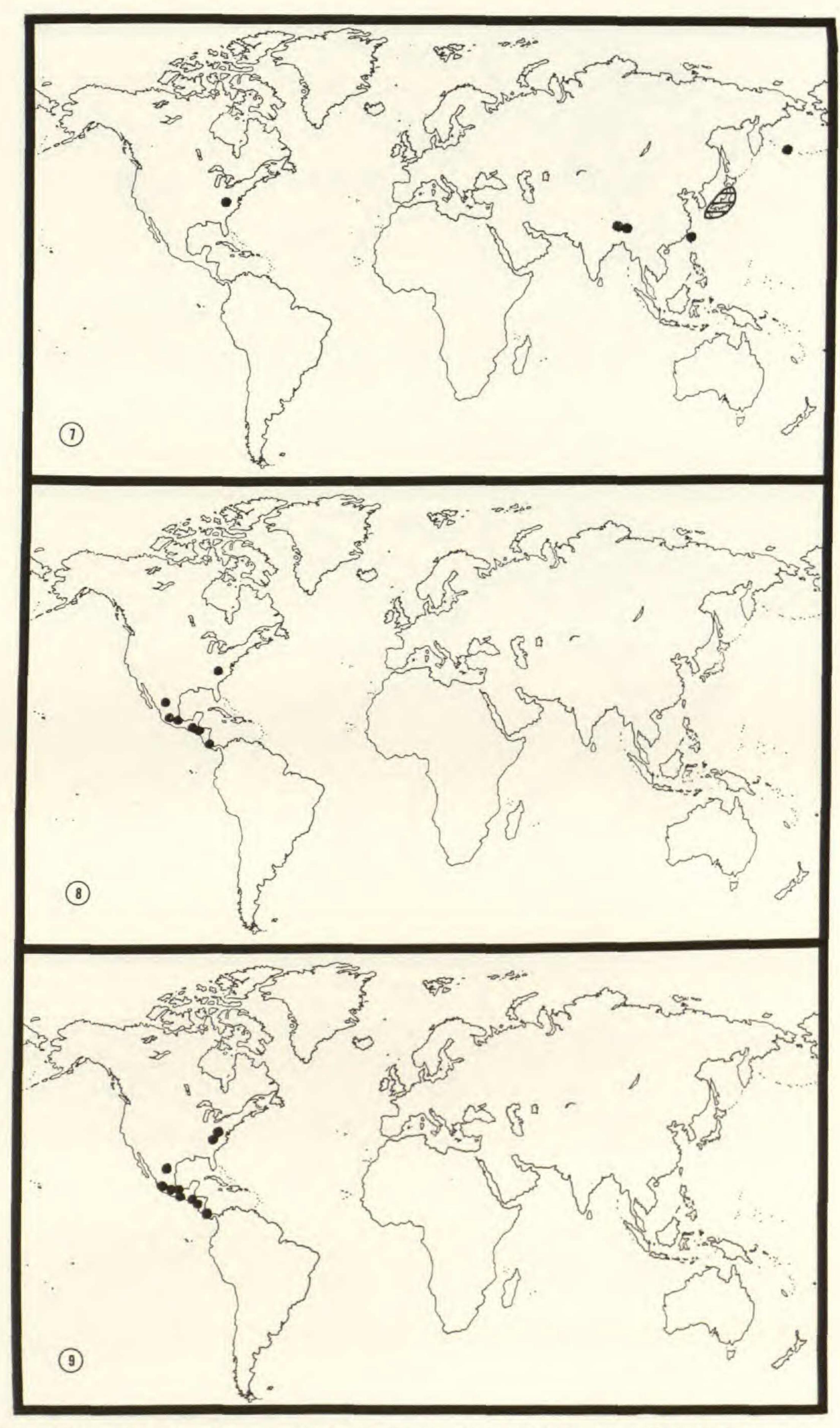
At present, then, there is no conclusive hypothesis that will explain all disjunctive distributions.



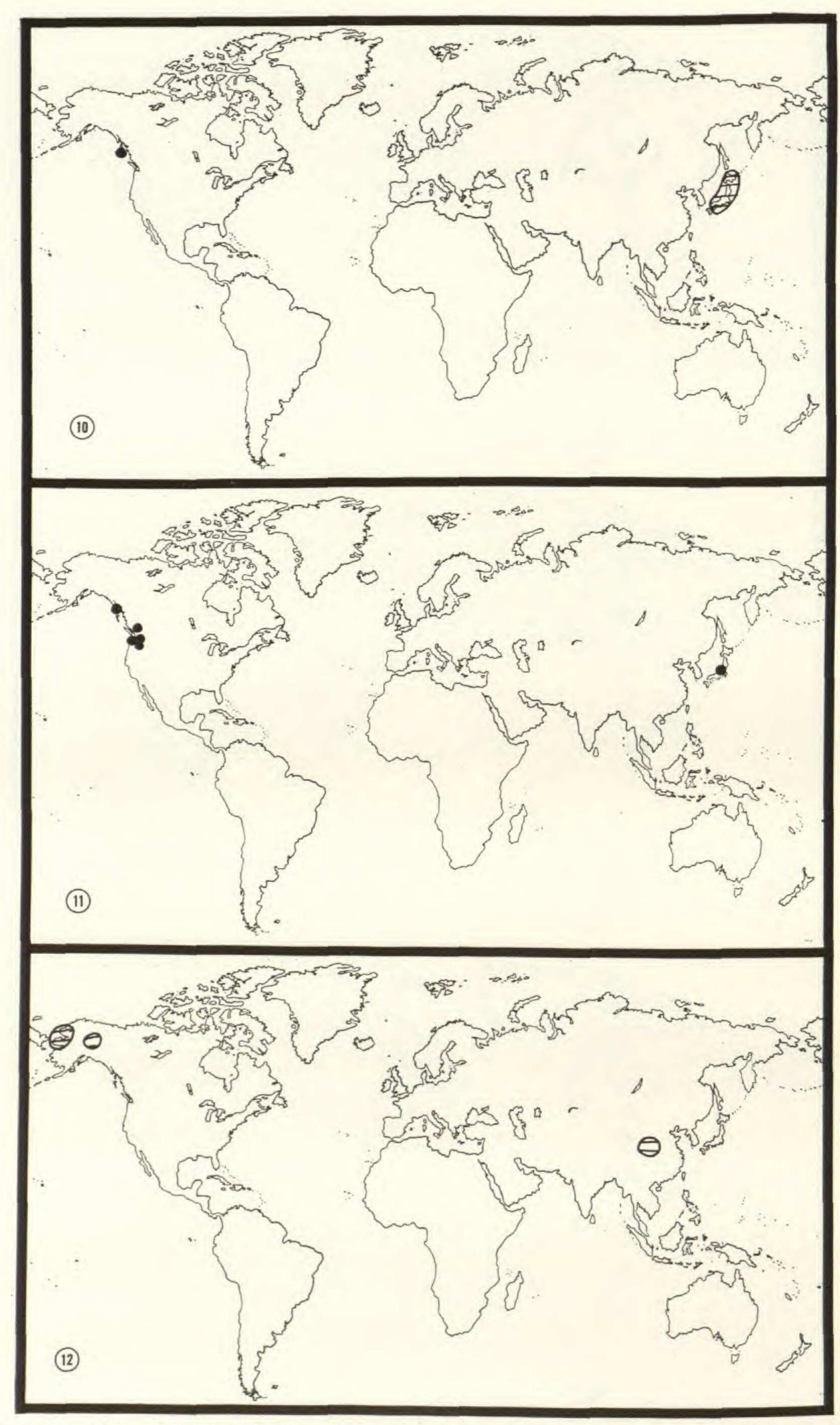
Maps 1–3.—Distribution of *Plagiochila japonica* Sande Lac. ex Miquel.—2. Distribution of *Homaliadelphus sharpii* (Williams) Sharp.—3. Distribution of *Drummondia prorepens* (Hedw.) Brid. (after Iwatsuki, 1958, in part).



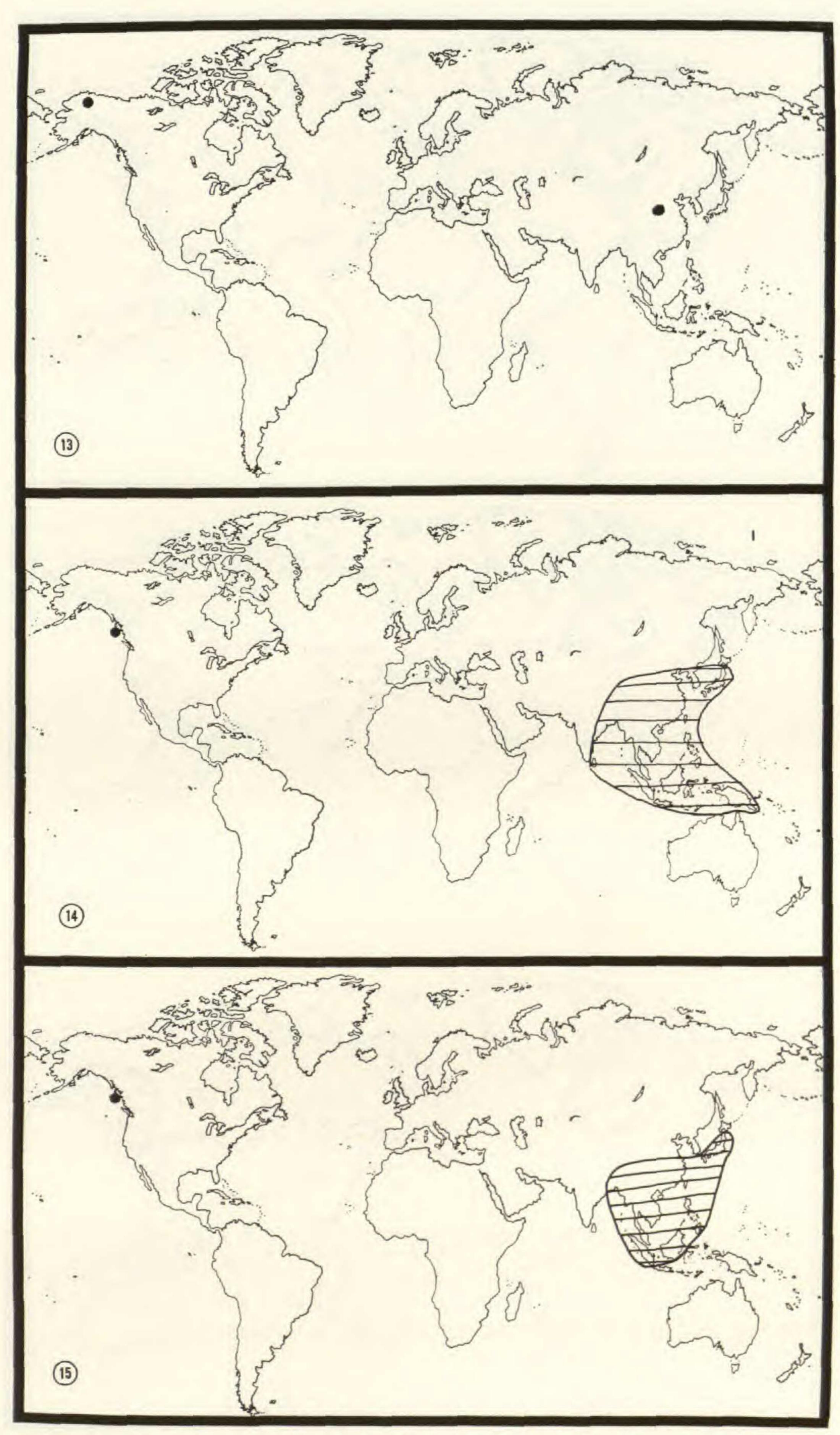
Maps 4–6.—4. Distribution of Aulacomnium heterostichum (Hedw.) B.S.G. (after Iwatsuki, 1958, expanded).—5. Distribution of Buxbaumia minakatae O. Okam. (after Iwatsuki & Sharp, 1967).—6. Distribution of Schwetschkeopsis fabronia (Schwaegr.) Broth. (after Iwatsuki & Sharp, 1967).



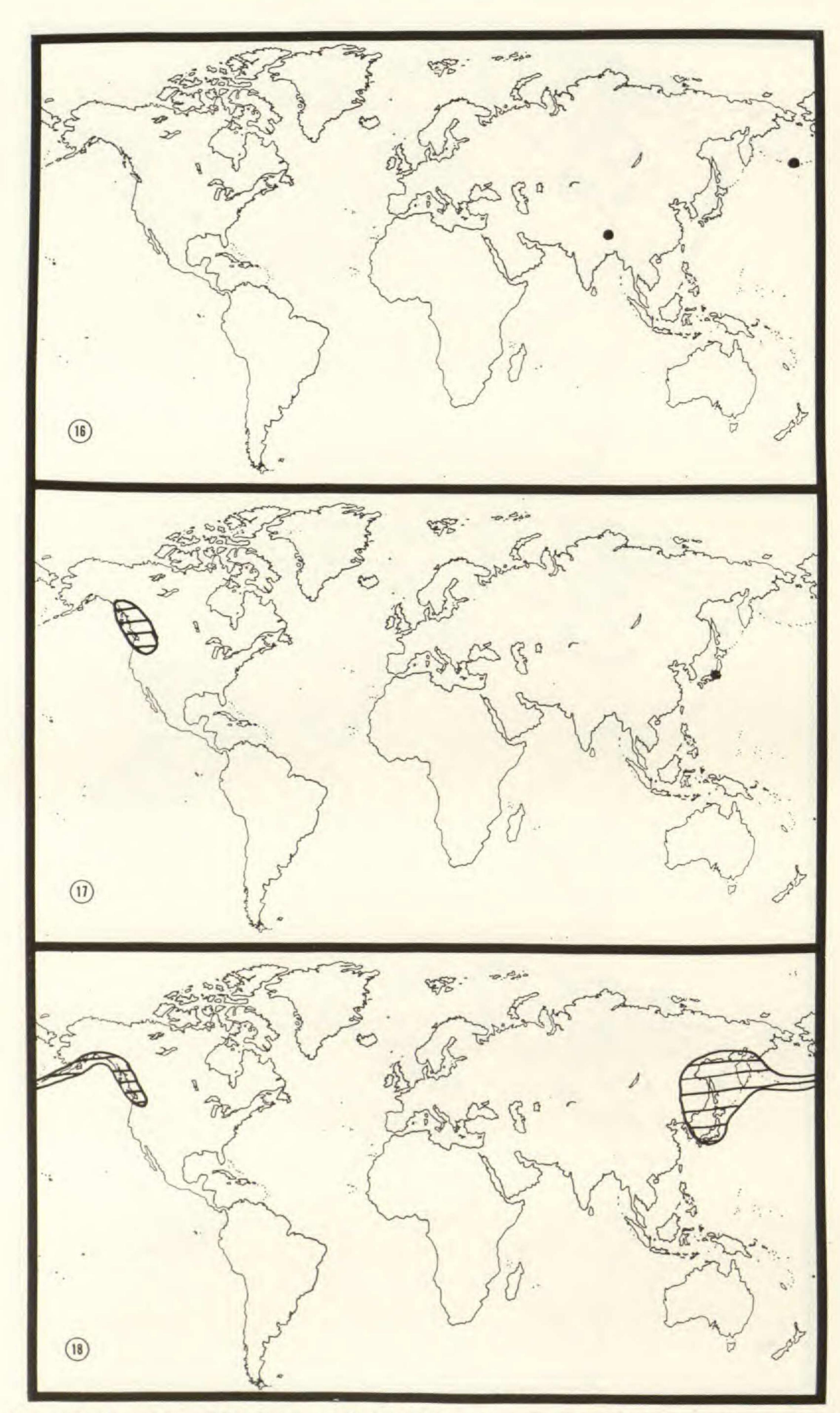
Maps 7–9.—7. Distribution of Acrobolbus ciliatus (Mitt.) Schiffn. (from information in Sharp & Hattori, 1968).—8. Distribution of Leptodontium orcuttii Bartr.—9. Distribution of Tortula caroliniana Andr.



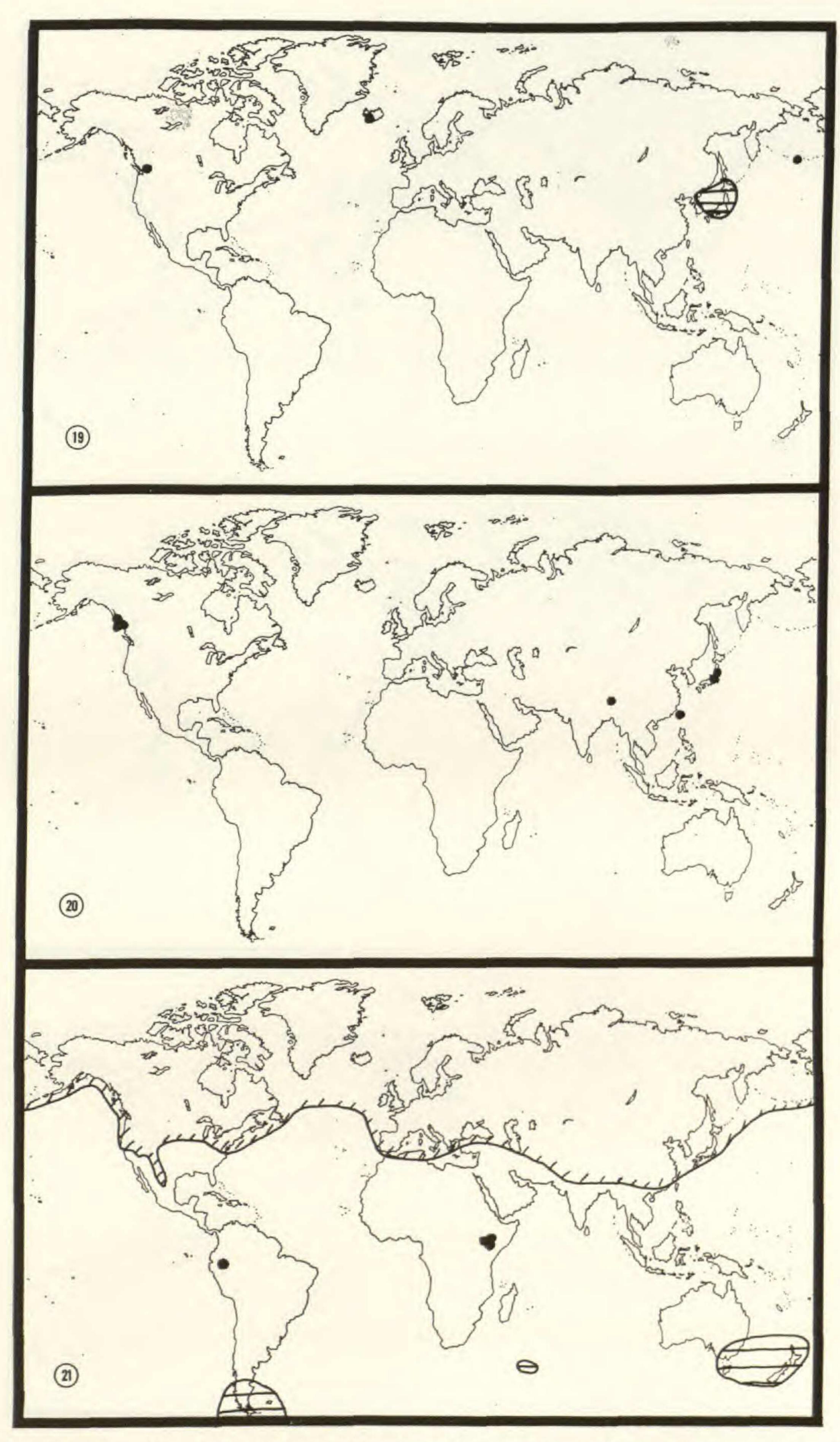
Maps 10–12.—10. Distribution of Radula auriculata Steph.—11. Distribution of Grimmia olympica Britt. ex Frye.—12. Distribution of Gollania turgens (C. Müll.) Ando (after Ando, Persson & Sherrard, 1957; Ando & Gjaervoll, 1961).



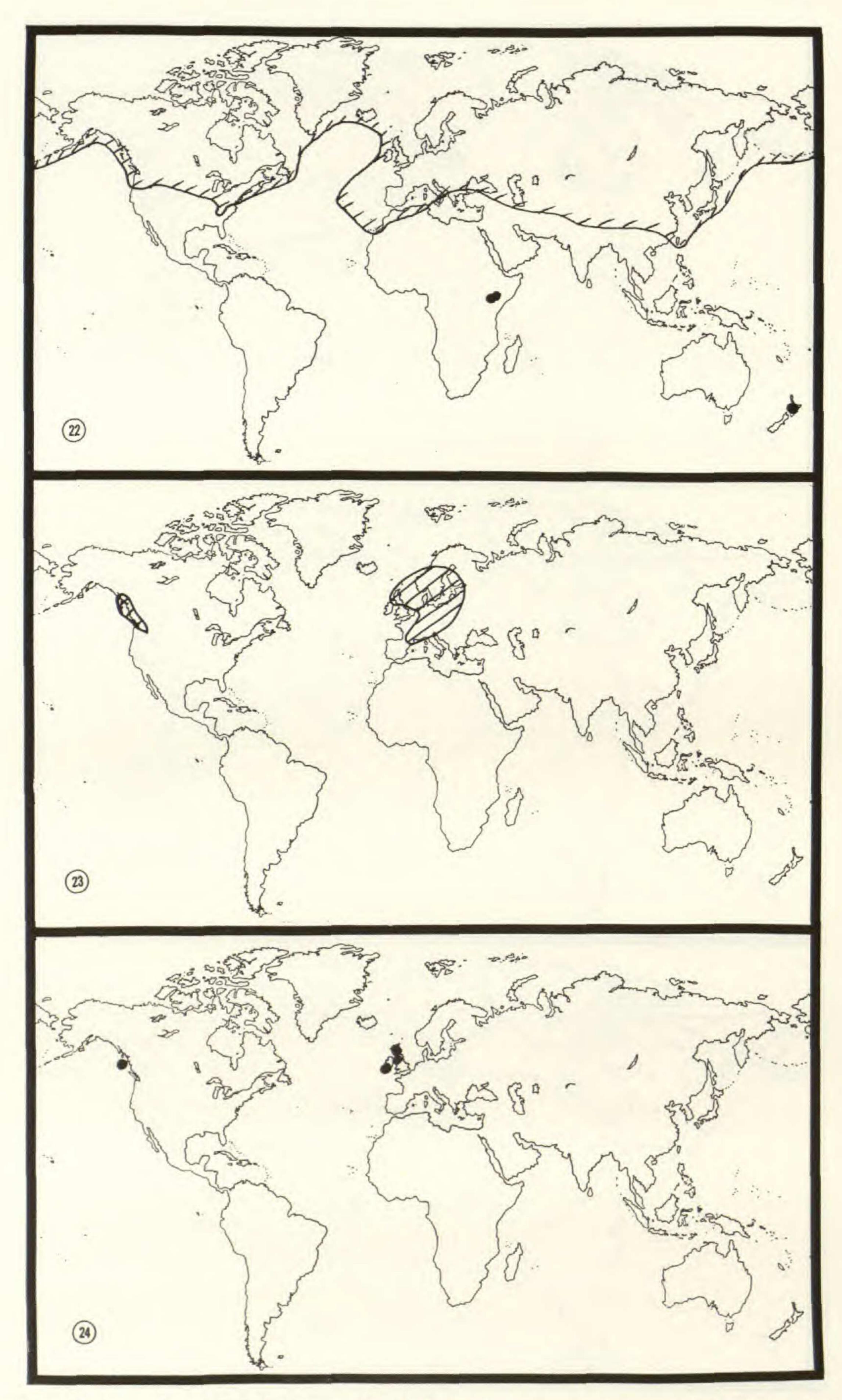
Maps 13-15.—13. Distribution of Ascidota blepharophylla Mass.—14. Distribution of Acanthocladium (Sect. Tanythrix).—15. Distribution of Sphagnum junghuhnianum Dozy. & Molk.



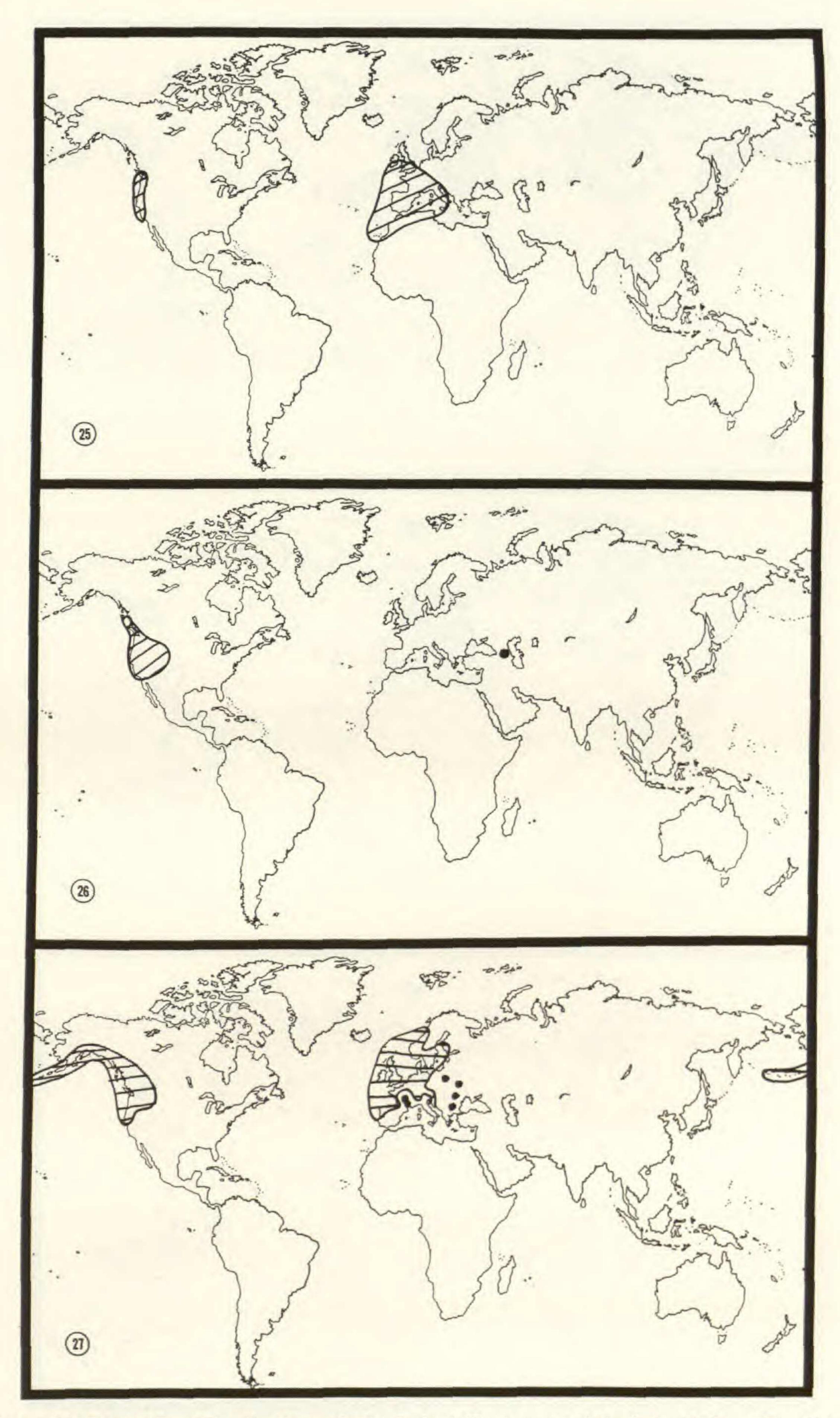
Maps 16–18.—16. Distribution of *Takakia ceratophylla* (Mitt.) Grolle (after Hattori et al., 1968).—17. Distribution of *Rhizomnium nudum* (Williams ex Britt. & Williams) Koponen.—18. Distribution of *Macrodiplophyllum plicatum* (after Horikawa, 1955, expanded).



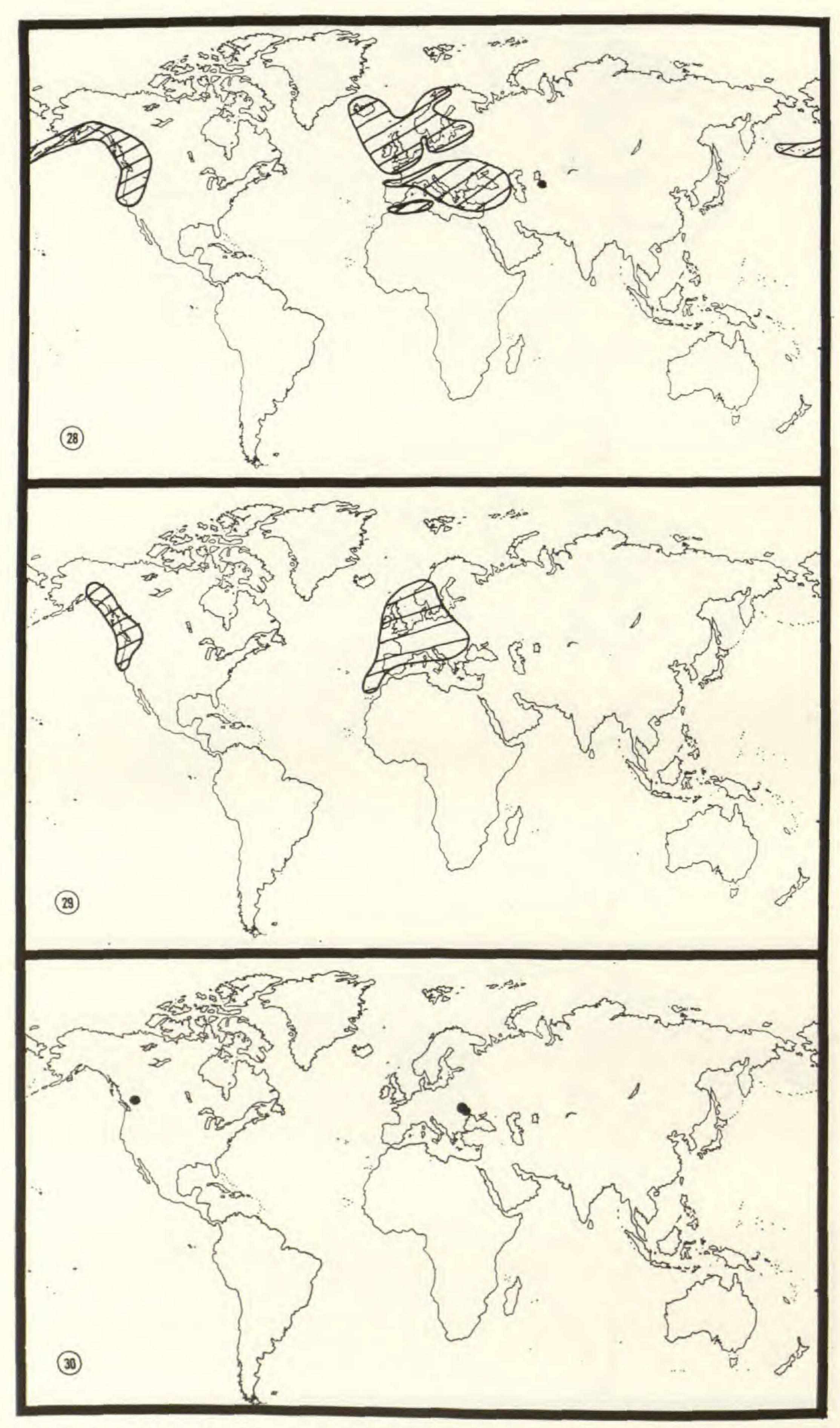
Maps 19-21.—19. Distribution of *Polytrichum sphaerothecium* (Besch.) Broth.—20. Distribution of *Treubia nana* Hatt. & Inoue (after Hattori *et al.*, 1966, expanded).—21. Distribution of *Drepanocladus uncinatus* (Hedw.) Warnst. (after Irmscher, 1929, expanded).



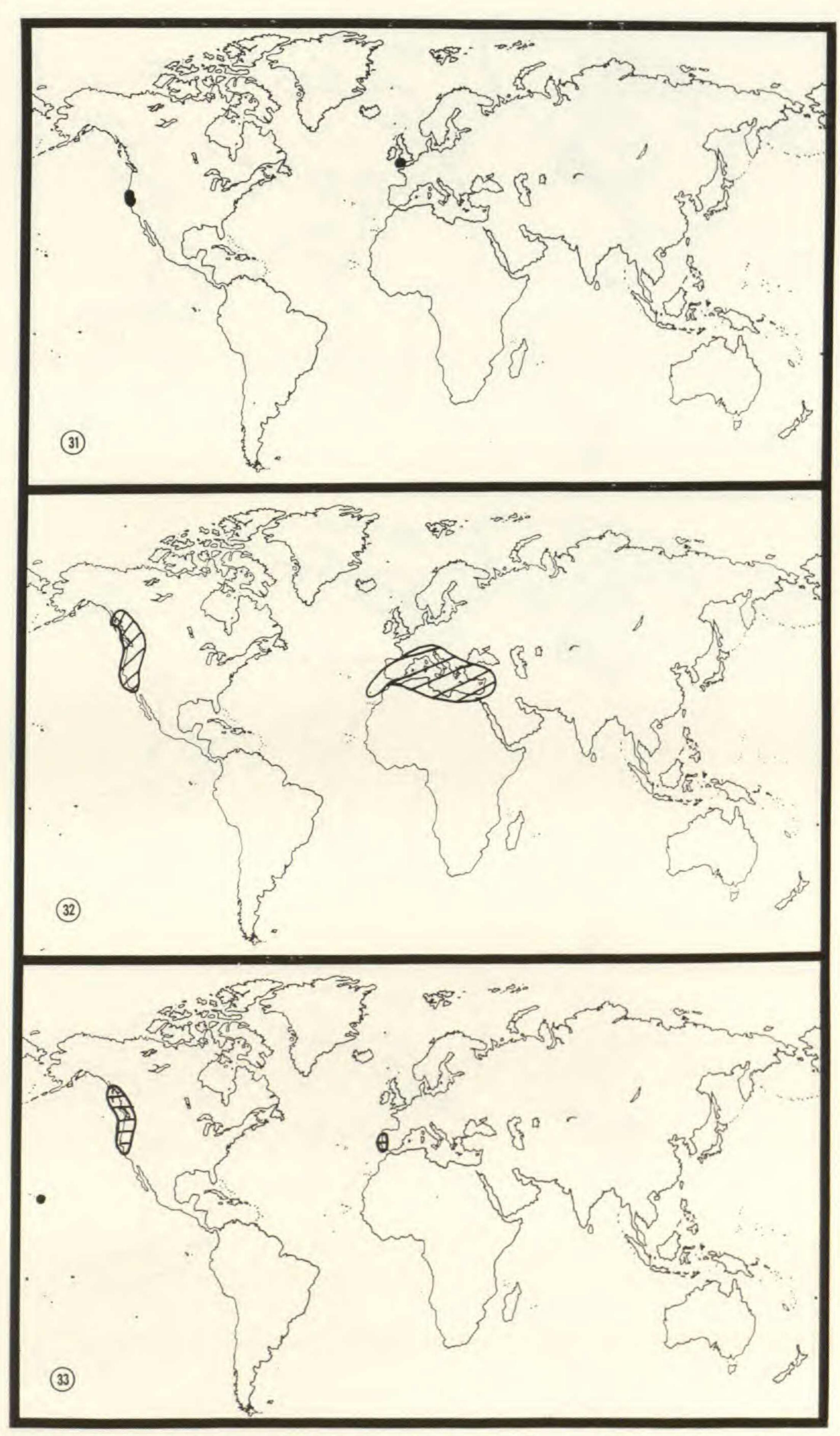
Maps 22–24.—22. Distribution of *Hylocomium splendens* (Hedw.) B.S.G.—23. Distribution of *Ditrichum zonatum* (Brid.) Kindb.—24. Distribution of *Leptodontium recurvifolium* (Tayl.) Lindb.



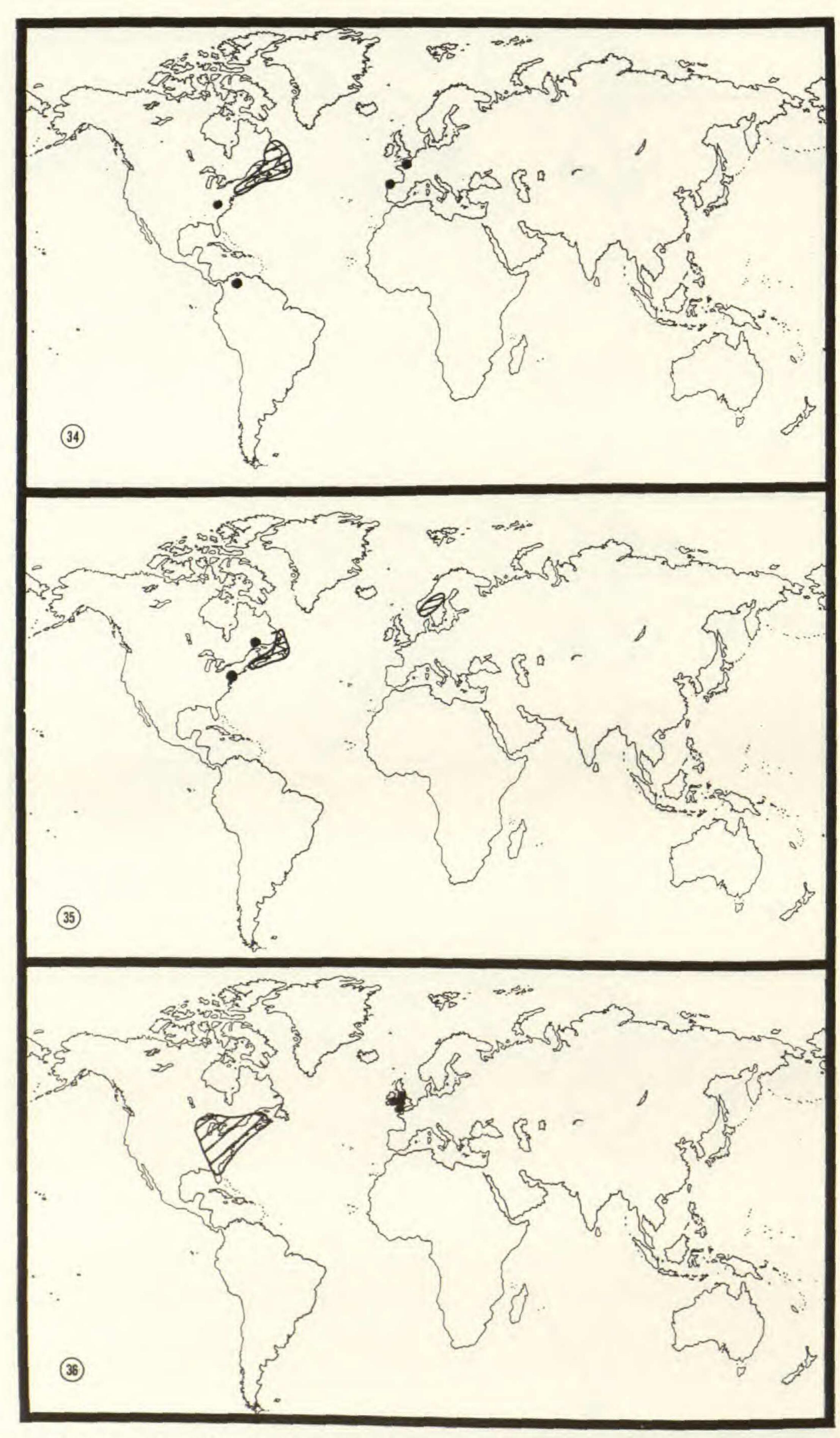
Maps 25–27.—25. Distribution of Cephaloziella turneri (Hook.) Müll.—26. Distribution of Crumia latifolia (Kindb. ex Mac.) Schof. (after Abramova & Dildarin, 1969).—27. Distribution of Plagiothecium undulatum (Hedw.) B.S.G. (after Ireland, 1969, Størmer, 1969).



Maps 28–30.—28. Distribution of *Porella cordaeana* (Hueb.) Evans (after Szwekowski, 1962).—29. Distribution of *Hookeria lucens* (Hedw.) Sm. (after Irmscher, 1929, modified; Størmer, 1969).—30. Distribution of *Bucegia romanica* Radian (after Szwekowski, 1964).

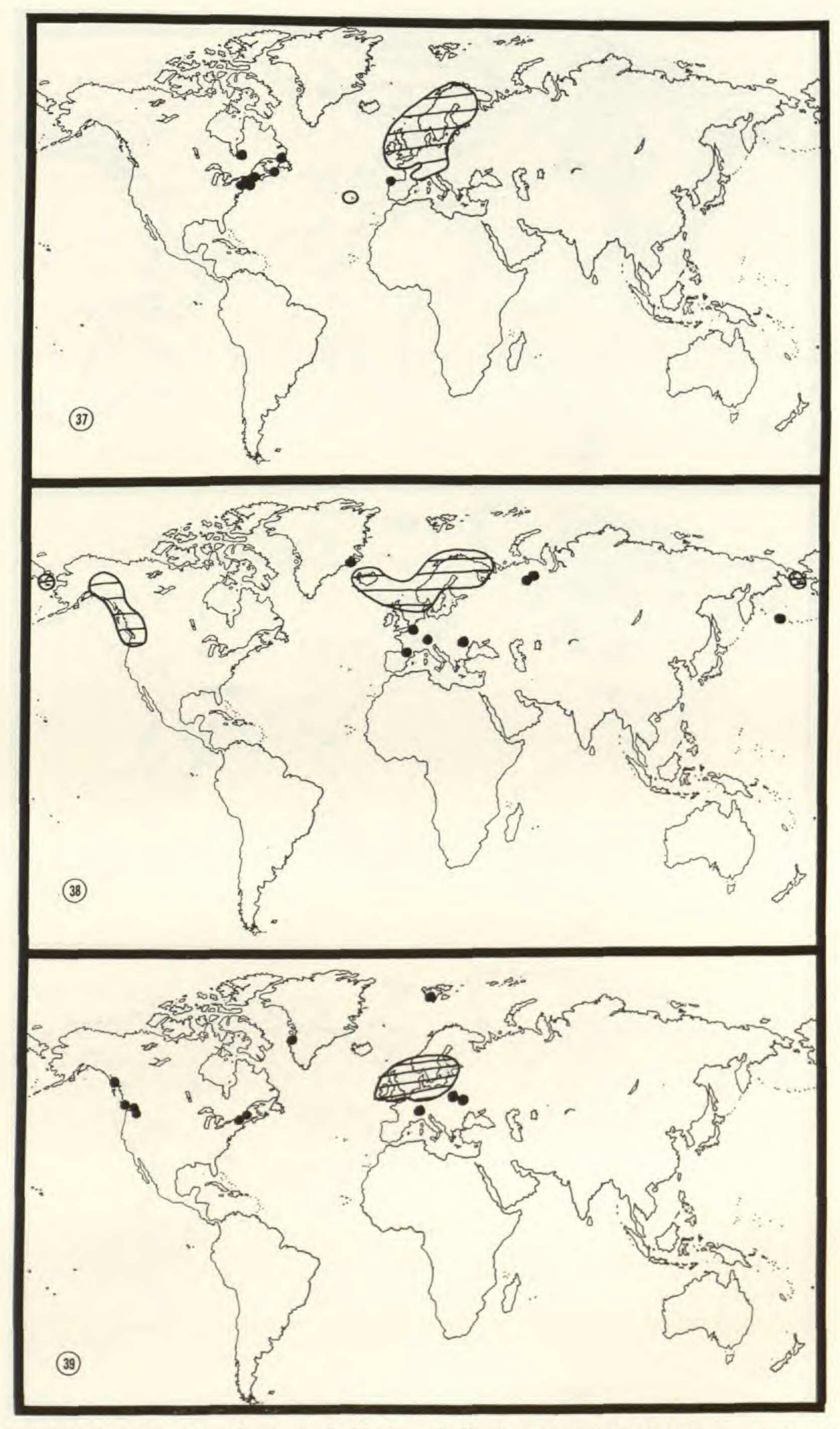


Maps 31–33.—31. Distribution of *Tortula standfordensis* Steere.—32. Distribution of *Antitrichia californica* Sull. ex Lesq.—33. Distribution of *Claopodium whippleanum* (Sull.) Ren. & Card. (from Noguchi, 1952, expanded).

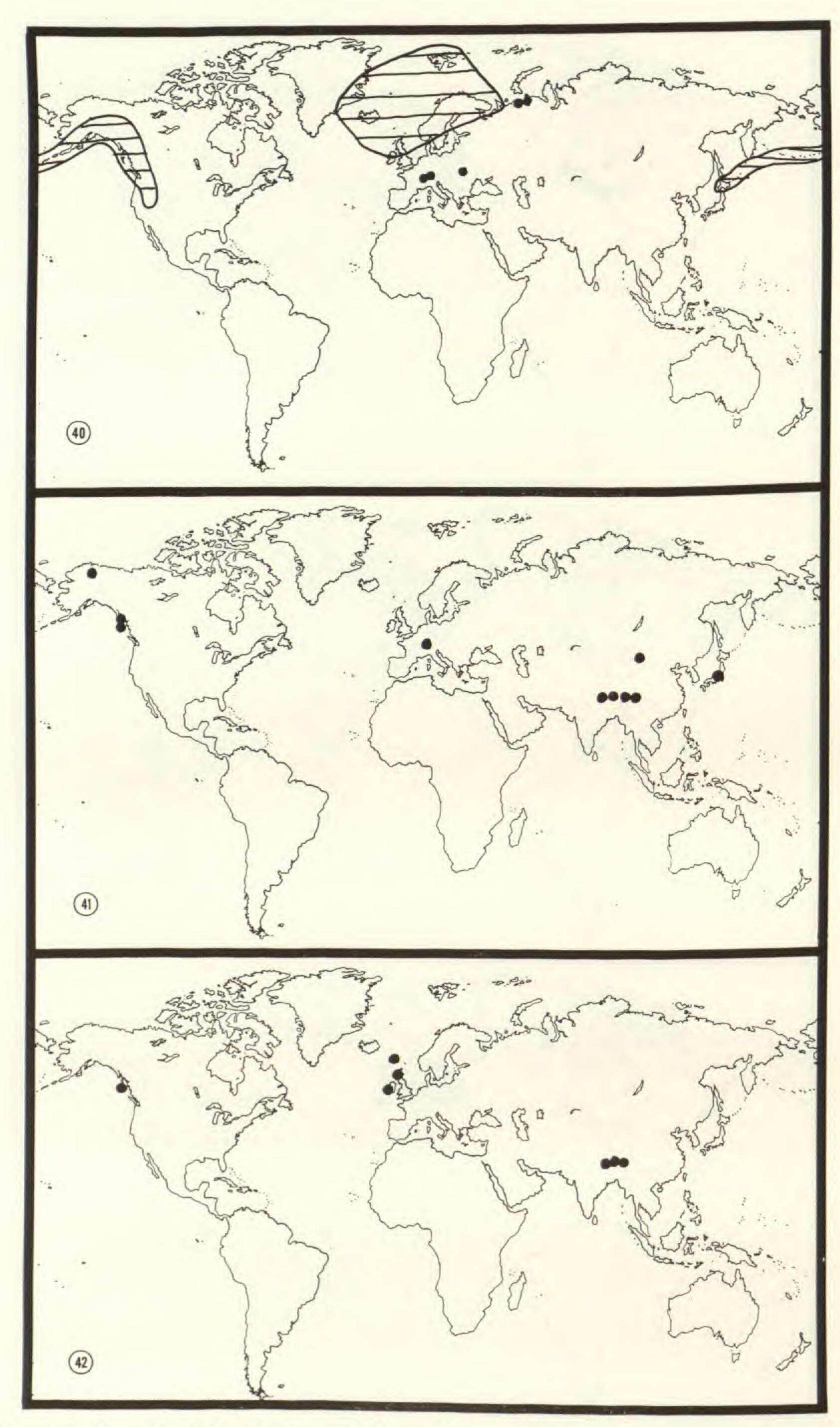


Maps 34-36.—34. Distribution of Sphagnum pylaesii Brid. (from Maass, 1966a, 1966b).

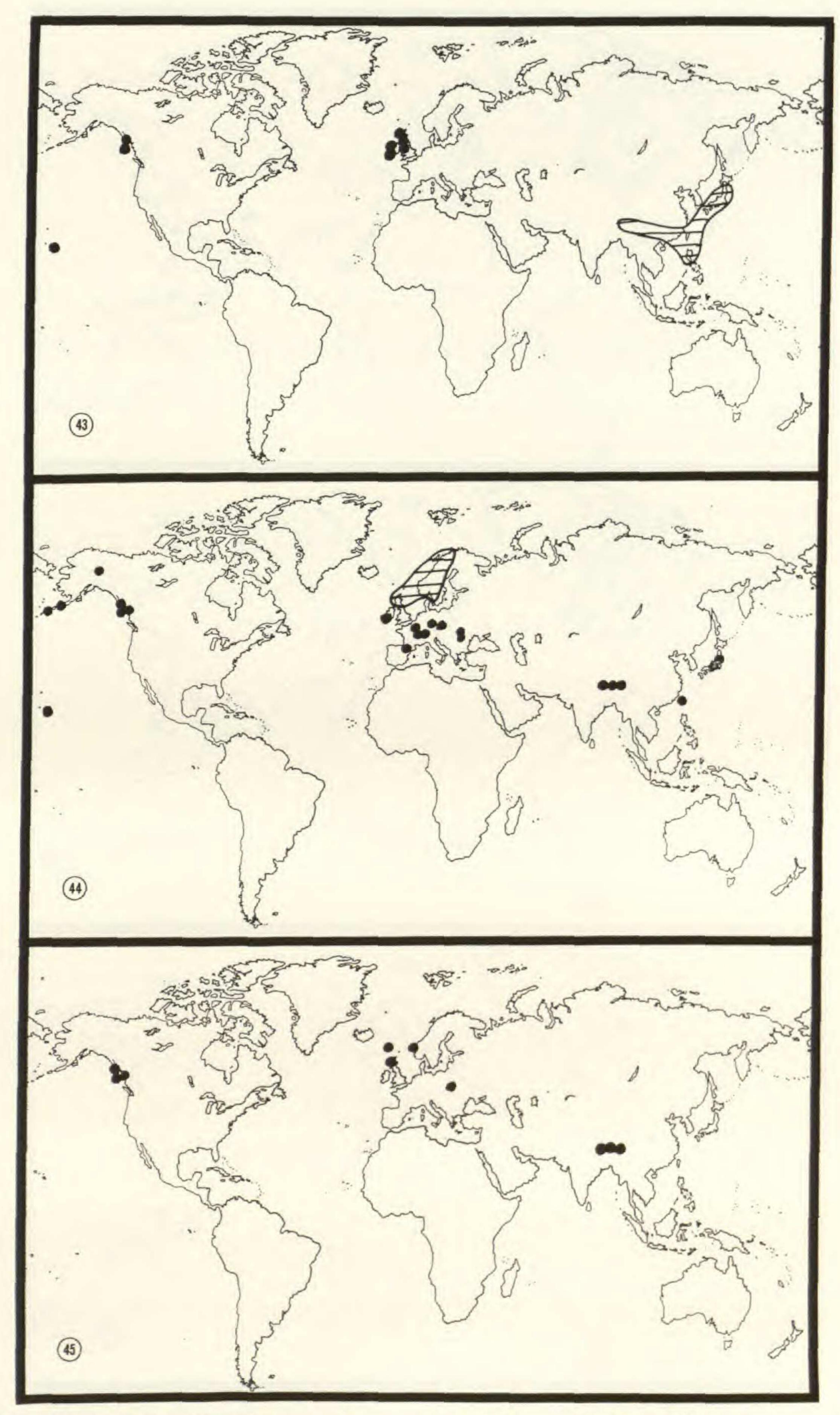
—35. Distribution of Sphagnum angermanicum Melin (supplied by W.S.G. Maass).—36. Distribution of Atrichum crispum (James) Sull. & Lesq. (after information in Ireland, 1969; Smith, 1966).



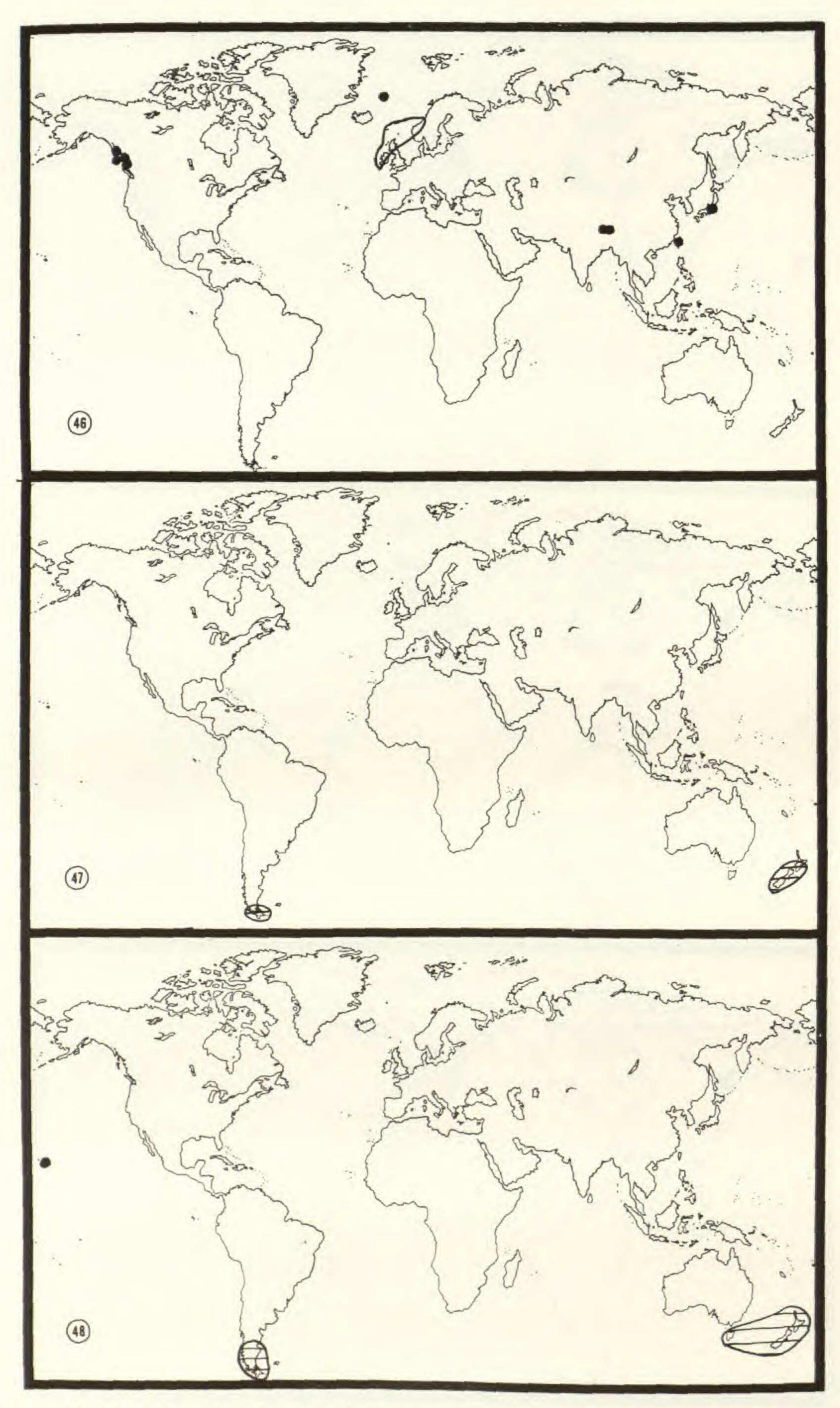
Maps 37–39—37. Distribution of Cladopodiella francisci (Hook.) Dum. (after Szwey-kowski, 1964, expanded).—38. Distribution of Oligotrichum hercynicum (Hedw.) Lam. & DC.—39. Distribution of Haplomitrium hookeri (Sm.) Nees (after Szweykowski, 1966, expanded; Corely, 1970).



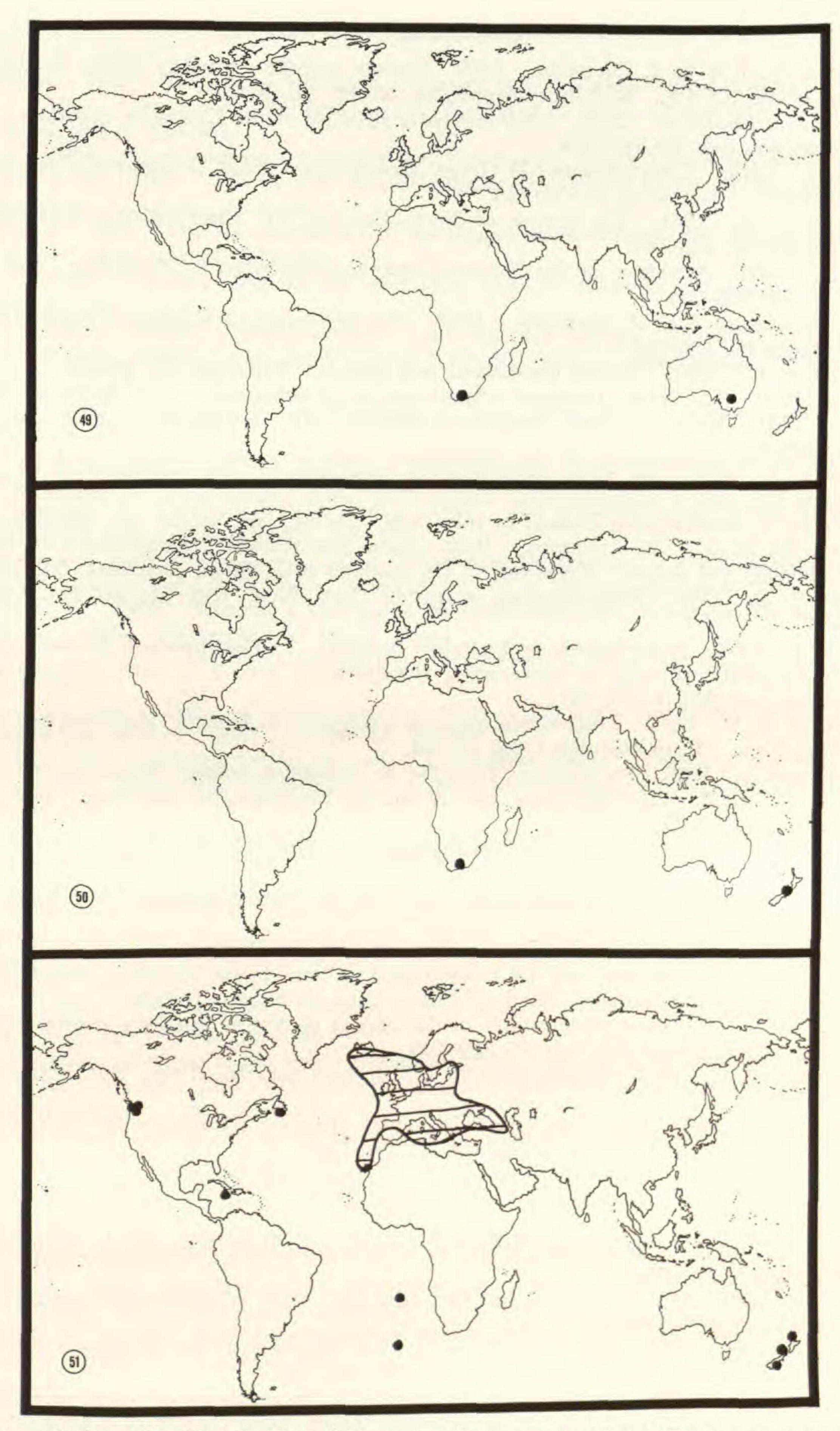
Maps 40—42.—40. Distribution of *Pleuroclada albescens* (Hook.) Spr. (after Szwey-kowski, 1966).—41. Distribution of *Geheebia gigantea* (Funck.) Boul.—42. Distribution of *Mastigophora woodsii* (after Ratcliffe, 1963, in part).



Maps 43–45.—43. Distribution of Scapania ornithopodioides (With.) Pears. (after Ratcliffe, 1965, in part).—44. Distribution of Anastrepta orcadensis (Hook.) Schiffn. (after Szweykowski, 1964, expanded).—45. Distribution of Anastrophyllum donianum (Hook.) Spr. (after Szweykowski, 1966, emended; Ratcliffe, 1965, in part).



Maps 46–48.—46. Distribution of *Pleurozia purpurea* (Lightf.) Lindb. (after Ratcliffe, 1969, in part).—47. Distribution of the genus *Phyllothallia* Hodgs. (after Schuster, 1969).—48. Distribution of *Cyrtopus setosus* (Hedw.) Hook.



Maps 49–51.—49. Distribution of Carros sphaerocarpos (Carr) Prosk.—50. Distribution of Pottia maritima (R. Br.) Broth. (after information in Schelpe, 1969).—51. Distribution of Pseudoscleropodium purum (Hedw.) Fleisch. (after Størmer, 1969, in part; Dickson, 1967).

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